

EVALUATION OF SALT TOLERANCE AND RESIN
PRODUCTION IN COASTAL AND CENTRAL VALLEY
ACCESSIONS OF *GRINDELIA* SPECIES (ASTERACEAE)

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ABSTRACT

The objective of this study was to evaluate the effect of NaCl on growth of *Grindelia* accessions from coastal and inland habitats. Gas exchange, biomass and resin production, and cation accumulation were studied for two accessions of *Grindelia stricta* from coastal estuaries, one accession of *G. camporum* from the northern part of the Central Valley, and one accession of *G. camporum* from the South Coast Ranges. A greenhouse experiment was conducted in which these accessions were grown for 140 days in sand culture at 5, 125, 250, and 550 mM (\approx sea water) NaCl. No major differences in salt tolerance were found between coastal and inland accessions—both species used in this study were found to be miohalophytes. Survival at 550 mM was 10% or lower for three of the four accessions. Gas exchange (net CO₂ uptake and transpiration) was reduced at salinities above 125 mM, and biomass production was significantly affected by salinity. However, we observed moderate growth rates at salinities up to 250 mM. We also noted a trend toward increased surface resin with increased salinity, but more experiments are needed to thoroughly evaluate this response. *Grindelia* is a potential crop plant which is tolerant to high salinity but our results indicate that biomass production would be significantly reduced if *Grindelia* were cultivated in saline soils.

RESUMEN

Se evaluó el efecto del NaCl sobre el crecimiento de cuatro entradas de *Grindelia* de ambientes costeros y mediterráneos. Se estudió el intercambio de gases, la producción de biomasa y resina, y la acumulación de cationes para dos entradas de *Grindelia stricta* provenientes de estuarios costeros, una entrada de *G. camporum* de la parte norte del Central Valley, y una entrada de *G. camporum* del South Coast Ranges. Se realizó un ensayo de invernáculo en el que se cultivaron estas entradas por 140 días en un medio de arena con 5, 125, 250, y 550 mM NaCl. No se encontraron diferencias significativas en cuanto a tolerancia a la salinidad entre entradas de la costa y tierra adentro—ambas especies usadas en este estudio podrían ser consideradas miohalófitas. Se observó supervivencia de 10% o menos en tres de las cuatro entradas a 550 mM NaCl. El intercambio de gases (absorción neta de CO₂ y transpiración) se redujo a niveles de salinidad superiores a 125 mM y la salinidad afectó significativamente la producción de biomasa. Sin embargo observamos un crecimiento moderado a salinidades de hasta 250 mM. También observamos una tendencia a aumento de la resina superficial al aumentar la salinidad, aunque se necesitan más experimentos para evaluar en profundidad esta respuesta. *Grindelia* es un cultivo potencial que es tolerante de altos niveles de salinidad, pero nuestros

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resultados indican que la producción de biomasa de *Grindelia* podría reducirse significativamente si se la cultiva en suelos salinos.

The genus *Grindelia* comprises approximately 60 species of annuals, perennials, and shrubs native to North and South America. Most North American species occur in arid and semiarid areas of the Southwest, Rocky Mountains states, and along the Pacific Coast. Six species of *Grindelia* (and several varieties) are currently recognized for California by Lane (1993); previously Munz (1968), based largely on the work of Steyermark (1934), recognized 11 species. Several taxa inhabit coastal marshes in California where they grow with other halophytic species such as *Salicornia virginica* L., *Spartina foliosa* Trin., *Jaumea carnosa* (Less.) A. Gray, and *Distichlis spicata* (L.) E. Greene, among others. Populations of *Grindelia camporum* E. Greene can be found in saline habitats in the Central Valley of California, associated with species of such salt-tolerant genera as *Atriplex*, *Suaeda*, *Distichlis*, and *Heliotropium*.

Grindelia species have been studied as potential crop plants because they produce a diterpenoid resin on the stems, leaves and involucre that may have value in the naval stores industry, with applications including inks, adhesives, tackifiers, and synthetic polymers (Hoffmann and McLaughlin 1986; Hoffmann et al. 1984). The production of surface resins by plants probably is an adaptation to aridity since most species that produce such resins are xerophytes (Hoffmann et al. 1984). Surface resins can protect leaves from excessive transpiration (Meinzer et al. 1990) and prevent the development of extreme leaf temperatures by increasing reflectance. More information is needed to better understand the ecological significance of surface resins and the effect of the environment, including salinity, on resin production.

Grindelia camporum, in particular, has been investigated as a potential crop for arid lands because it combines a high resin content (Timmermann et al. 1987) with good biomass yield and relatively low irrigation requirement (McLaughlin and Linker 1987). Tolerance of high soil salinity would also be a valuable trait in a new crop because it would permit its cultivation in areas where soils have degraded due to salinization. Salt tolerance in *G. camporum* likely could be improved by selection among accessions for salt tolerance. Alternatively, increased salt tolerance might be incorporated into *G. camporum* by hybridization with coastal salt-marsh *Grindelia* species that presumably have greater salt tolerance.

Based on their occurrence in saline habitats, some *Grindelia* species are clearly able to tolerate moderate to high salt concentrations in the soil. However, the manner in which salt affects their growth is not known. Growth could be depressed as in miohalophytes which tolerate salt but have optimum growth on fresh water, or it could be

stimulated by NaCl in concentrations as high as 200 mM (about two fifths of that of sea-water) as in euhalophytes (Glenn and O'Leary, 1984). Furthermore, the effect of NaCl concentration on the secretion of resin is not known.

To better understand salt tolerance in *Grindelia*, we studied the influence of NaCl on growth, gas exchange, cation content, and resin in four accessions. We were particularly interested in comparing the salt tolerance of coastal and inland taxa. We selected accessions that we believed should show a range of variation in their response to salt: two came from coastal estuaries, one was from the northern part of the Central Valley, and one was from the South Coast Ranges. We hypothesized that the salt-marsh accessions would prove to be euhalophytes, that the Central Valley accession would be a miohalophyte, and that the South Coast Range accession would have the lowest salt tolerance.

MATERIALS AND METHODS

Plant materials. Four accessions were included in this experiment: *G. camporum* var. *camporum* (SPM 6547; 2N = 24), collected in the Sacramento River Valley along State Route 20 east of I-5 in Colusa County; *G. camporum* var. *camporum* (SPM 6560; 2N = 24), collected in the South Coast Range east of Highway 101 on State Route 58 near Santa Margarita in San Luis Obispo County; *G. stricta* DC. var. *stricta* (SPM 6548; 2N = 24), collected from an estuary of Humboldt Bay adjacent to Elk River Road east of Highway 101 in Humboldt County; and *G. stricta* var. *platyphylla* (E. Greene) M. A. Lane (SPM 6558; 2N = 24), collected from an estuary just north of Moss Landing along State Route 1 in Monterey County. The collections of *Grindelia camporum* var. *camporum* from near Colusa and Santa Margarita will be referred to as *G. camporum* COL and *G. camporum* SM, respectively. Bulk seed collections, obtained by gathering seed from several plants in each population, were made between 22 and 25 September 1991. Voucher specimens were deposited at ARIZ.

Experimental conditions. Seeds were germinated in the greenhouse in 1-in. pots containing sand and peat moss (1:1 by volume) after a pre-treatment of one week in water at 3°C with exposure to light. Greenhouse temperatures ranged between 32°C during the day and 12°C during the night. Three weeks after germination, 40 plants of each accession (for a total of 160 plants) were transplanted to 1-gal pots filled with pure sand. Irrigation with ½ Hoagland solution (Hoagland and Arnon 1938) was initiated three days after transplanting.

Plants were randomly assigned to one of four salt treatments: 5 mM NaCl, 125 mM NaCl, 250 mM NaCl, and 550 mM NaCl; the

latter is equivalent to the salt levels in sea water. NaCl (analytical reagent) was added at increments of 50 mM/day, starting on 31 August. Final salt concentrations were reached on 31 August, 2 September, 4 September, and 10 September for the 5, 125, 250, and 550 mM treatments, respectively. All plants were irrigated with a solution that included $\frac{1}{2}$ Hoagland solution and the NaCl at the assigned level. Solution pH was measured each time fresh solution was prepared and ranged from 6.4 to 6.5 for all solutions. Pots were irrigated three times/day with 150 ml of solution each time to allow for leaching and to prevent salt accumulation in the pots.

Gas exchange measurements. Net CO₂ uptake and transpiration were measured on 8 November on five plants of each accession growing at 5, 125, and 250 mM, using an ADC-LCA3 portable infrared gas-exchange system (Analytical Development Company, Hoddesdon, England). For the 550 mM treatment gas exchange could only be measured on *G. s. var. stricta* since there were not enough plants alive of the other accessions to permit repeated measurements. All measurements were taken in the greenhouse between 11:00 AM and 12:30 PM.

Biomass production. Five plants per species per treatment were harvested on 2 November and 28 December, 84 and 140 days, respectively, after highest salinity was reached. The aboveground portion of *Grindelia* plants consists initially of basal rosettes from which one or more leafy reproductive stems eventually bolt. Here we report all aboveground biomass as "shoots." Harvested plants were air-dried to constant weight in the greenhouse for seven to ten days after which dry weights of both shoots (DWS) and roots (DWR) were recorded. At each harvest date the numbers of bolted stems, flower-buds, and flowers at or beyond anthesis were recorded.

Resin extraction. Above-ground biomass of each harvested plant was ground to 3-mm particle-size and a 3- to 5-g subsample was extracted twice with 150 ml of dichloromethane at room temperature for 24 hr. The crude extracts were evaporated and the total crude resin yields were determined as percentage of dry biomass.

Determination of cations. Samples (0.05 g) of shoot and root tissues from the first (2 November 1994) harvest were digested overnight in concentrated nitric acid and then heated for an hour at 100 C. Na⁺, K⁺, Ca²⁺, and Mg²⁺ were determined by atomic absorption spectroscopy (Association of Official Analytical Chemists, 1984).

Statistical analysis. A factorial analysis of variance (ANOVA) with accessions (4 levels) and salt concentration (3 levels for most ANOVAs since few plants survived at 550 mM NaCl; see Results) as the main factors was done for each variable measured. The num-

ber of replicates was $n=5$ for each treatment combination. Mean separation was done using Duncan's Multiple Range test.

RESULTS

Survivorship. No mortality was observed in any accession with NaCl concentrations up to 250 mM. At 550 mM all 10 *G. s. var. stricta* plants were alive (100% survival) at 84 days, but only six *G. s. var. platyphylla*, four *G. camporum* COL, and two *G. camporum* SM (60%, 40%, and 20% survival, respectively) plants survived. At this first sampling date, five of the ten *G. s. var. stricta* plants were harvested. Surviving plants of the other accessions were not harvested to permit continued observations on survival. When the experiment was terminated at 140 days, three of the five unharvested *G. s. var. stricta* plants from the 550 mM NaCl treatment were alive (60% survival), but only one plant each of *G. s. var. platyphylla* and *G. camporum* COL survived; none of the 10 plants of *G. camporum* SM survived.

Gas exchange measurements. Averaged over the four accessions, net CO₂ uptake (A) was significantly reduced by salt concentrations higher than 125 mM ($F = 8.46$, $P < 0.01$; Fig. 1a). The four *Grindelia* accessions used in this experiment did not differ significantly in their photosynthetic response to salt, although the A rates of all *G. s. var. stricta* plants at 550 mM NaCl were higher than that of the one plant of *G. camporum* COL surviving at this salinity. Transpiration (E) was significantly affected by NaCl concentration levels above 125 mM ($F = 11.26$, $P < 0.01$; Fig. 1b) and differed among accessions ($F = 5.51$, $P < 0.01$). Transpiration rates peaked at 125 mM for all accessions but *G. camporum* SM. Overall, *G. camporum* SM showed significantly higher E rates than the other three accessions. Significant reductions in stomatal conductance (Gs) were found at NaCl concentrations above 125 mM ($F = 16.93$, $P < 0.01$; Fig. 1c), but the four *Grindelia* accessions did not differ in stomatal conductance averaged across salt treatments.

Biomass production. At first harvest, 84 days after the highest salinity was reached, DWS ($F = 44.91$, $P < .01$; Fig. 2a), DWR ($F = 32.68$, $P < .01$; Fig. 2b), and DWT (total dry weight) ($F = 41.48$, $P < .01$) were significantly affected by salt treatments in all *Grindelia* accessions. Increased salinity resulted in proportionally larger percentage reductions in DWR than in DWS, although NaCl concentration did not have a significant effect on shoot:root (S:R) ratio at the first harvest. The accessions differed significantly in their S:R ratios ($F = 8.43$, $P < 0.01$, Fig. 2c), however; *G. s. var. platyphylla* had the highest S:R ratio and *G. camporum* SM had the lowest S:R ratio.

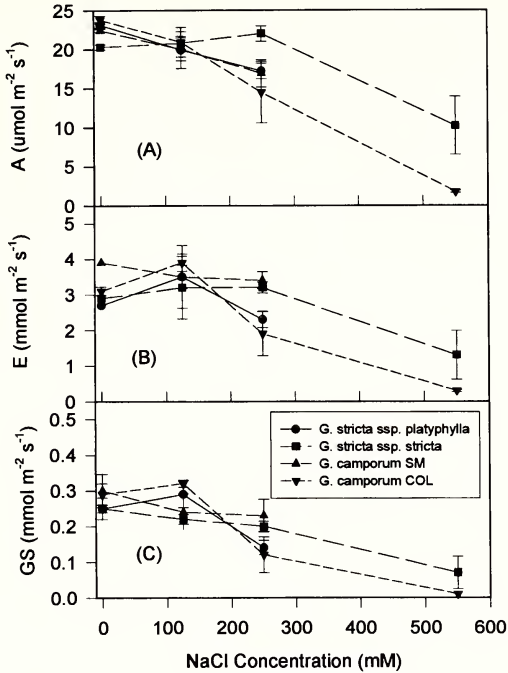


FIG. 1. Effect of NaCl on gas exchange in four *Grindelia* accessions: (A) net CO₂ uptake; (B) transpiration; (C) stomatal conductance. Error bars represent ± 1 SE of the mean; n=5.

At the second harvest date, 140 days after maximum salinity was reached, NaCl had a significant effect on DWS ($F = 102.84$, $P < 0.01$; Fig. 3a), DWR ($F = 115.04$, $P < 0.01$; Fig. 3b), and DWT ($F = 135.54$, $P < 0.01$). Accessions differed in their response to NaCl ($F = 9.83$, $P < 0.01$). *Grindelia s. var. platyphylla* had significantly higher DWS production than the other three accessions; *G. s. var. stricta* had the lowest DWS. Both *G. s. var. platyphylla* and *G. camporum COL* had a significantly higher DWR than *G. s. var. stricta* and *G. camporum SM* at 5 mM NaCl ($F = 8.06$, $P < 0.01$; Fig. 3b). The percentage reductions in DWS, DWR, and DWT at 125 mM NaCl and 250 mM were similar for all four accessions. One of the few clear differences found between estuarine and inland *Grindelia* accessions used in this study was that both varieties of *G. stricta* had significantly larger ($F = 11.50$, $P < 0.01$; Fig. 3c) S:R ratios at 140 days than both accessions of *G. camporum*. In the *G. stricta* varieties S:R ratios were higher at 125 mM than at 5 mM, while in the *G. camporum* accessions S:R ratios decreased with increasing salinity ($F = 11.50$, $P < 0.01$).

The number of stems bolting per plant at 84 days was significantly

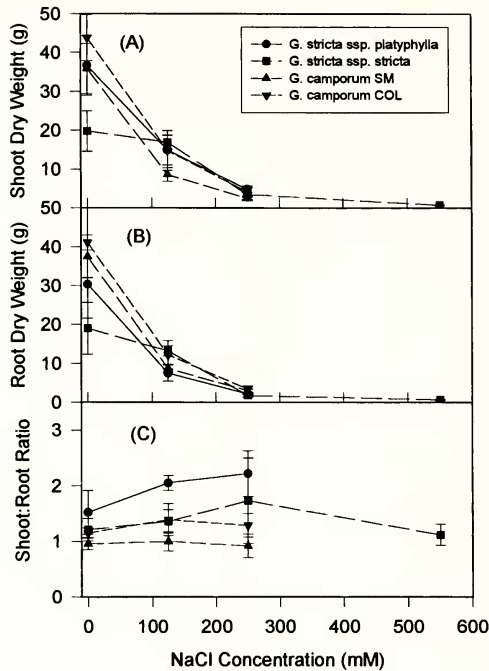


FIG. 2. Effect of NaCl on biomass accumulation of four *Grindelia* accessions measured 84 days after highest salinity was reached: (A) shoot dry weight; (B) root dry weight; (C) shoot:root ratios. Error bars represent ± 1 SE of the mean; $n=5$.

affected by NaCl concentration ($F = 34.61$, $P < 0.01$; Fig. 4a). *Grindelia s. var. platyphylla* and *G. camporum COL* had more stems per plant than the other two accessions ($F = 15.76$, $P < 0.01$). At 250 mM all *G. camporum COL* plants had bolted, all *G. camporum SM* plants were still in the rosette stage, and only one *G. s. var. platyphylla* and one *G. s. var. stricta* had produced stems (with 4 and 1 stem, respectively). The number of stems per plant at 140 days also decreased with increasing NaCl concentrations ($F = 10.82$, $P < .01$, Fig. 4b). There were also significant differences between accessions ($F = 2.92$, $P < .05$); both *G. camporum* accessions had more shoots per plant than the two *G. stricta* varieties. At 140 days only plants of the two *G. camporum* accessions had produced many flowers. Differences in numbers of flowers were noted among plants of the two accessions—*G. camporum COL* plants had an average of 15.2, 9.0, and 0 capitula per plant at 5 mM, 125 mM, and 250 mM NaCl, respectively, while those of *G. camporum SM* had 23.4, 19.6, and 1.0 capitula per plant at these salinity levels.

Resin production. A significant effect of NaCl concentration on crude resin production was found on plants harvested 84 days after

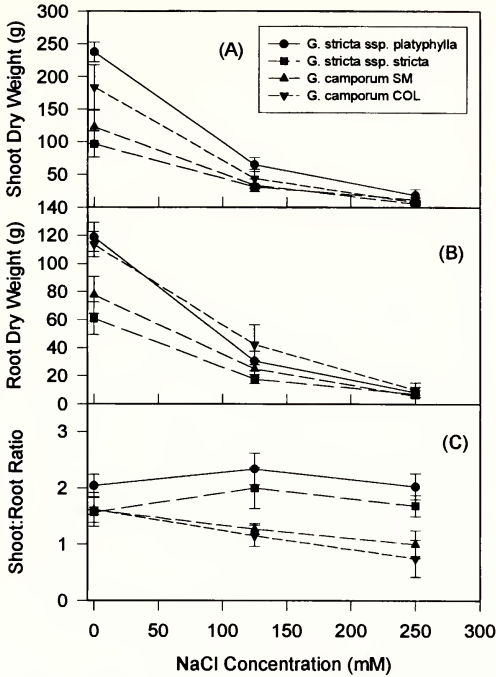


FIG. 3. Effect of NaCl on biomass accumulation of four *Grindelia* accessions measured 140 days after highest salinity was reached: (A) shoot dry weight; (B) root dry weight; (C) shoot:root ratios. Error bars represent ± 1 SE of the mean; $n=5$.

higher salinity was reached ($F = 5.45$, $P < 0.01$; Fig. 5a). The highest levels of crude extracts were found at 250 mM NaCl for *G. camporum* COL. Crude resin content was highest on plants grown at low NaCl levels in *G. camporum* SM, while there was no significant effect of NaCl on resin production in *G. s.* var. *stricta*. At 140 days there appeared to be a trend of increased crude resin content with increased salinity for all accessions but *G. stricta* var. *stricta* (Fig. 5b), although the differences were not statistically significant.

There were significant differences between accessions in crude resin contents both at 84 days ($F = 49.8$, $P < 0.01$) and at 140 days ($F = 18.1$, $P < 0.01$). Averaged across salt treatments, crude resin contents were highest for *G. camporum* COL and lowest for *G. stricta* var. *stricta*. Timmermann et al. (1987) reported the same pattern for plants sampled from the wild: high crude resin contents from plants in the Colusa population of *G. camporum*; low crude resin contents from plants in the Humboldt Bay population of *G. stricta* [reported in Timmermann et al. (1987) as *G. stricta* ssp. *blakei* (Steyserm.) Keck]; and intermediate crude resin contents in *G.*

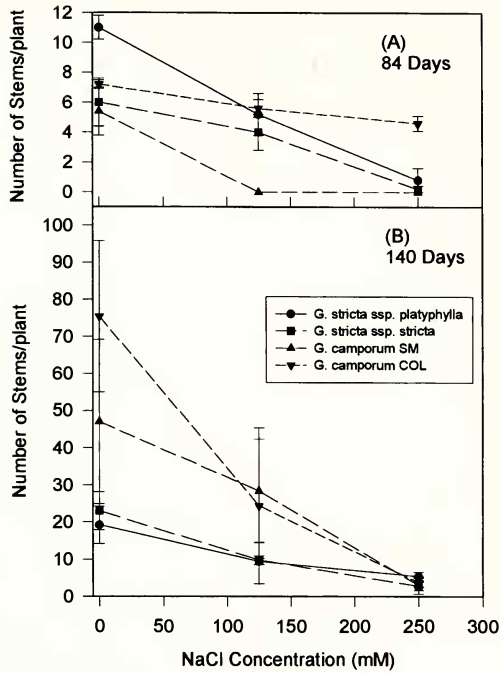


FIG. 4. Effect of NaCl on the number of stems per plant of four *Grindelia* accessions: (A) 84 days and (B) 140 day after highest salinity was reached. Error bars represent ± 1 SE of the mean; $n=5$.

camporum plants from Santa Margarita and *G. stricta* var. *platyphylla* [reported as *G. latifolia* Kell. ssp. *platyphylla* (Greene) Keck].

Cation contents. The general patterns of cation concentrations were similar for both roots and shoots: $[Na^+]$ increased, $[Ca^{2+}]$ decreased (drastically in the case of roots), and shoot $[K^+]$ decreased (Table 1). $[Mg^{2+}]$ and the ratio $[K^+]:[Na^+]$ also decreased as NaCl level increased from 5 mM to 125 mM ($P < 0.01$ for all cations; Table 1). Few significant differences were found in root cation concentrations in plants grown at 125 mM and 250 mM, except that $[Ca^{2+}]$ decreased for all four accessions and $[Na^+]$ and $[K^+]$ decreased in *G. s.* var. *platyphylla*.

The accessions differed in root $[Na^+]$, $[K^+]$, and $[Mg^{2+}]$, but not in $[Ca^{2+}]$. $[Na^+]$ and $[Mg^{2+}]$ were higher in *G. s.* var. *stricta* roots than in the other three accessions ($P < 0.01$). An interaction between NaCl concentration and accession was found for $[K^+]$ ($P < 0.01$)—as NaCl increased, $[K^+]$ fluctuated in *G. camporum* COL and *G. s.* var. *platyphylla*, and decreased in *G. s.* var. *stricta* and *G. camporum* SM.

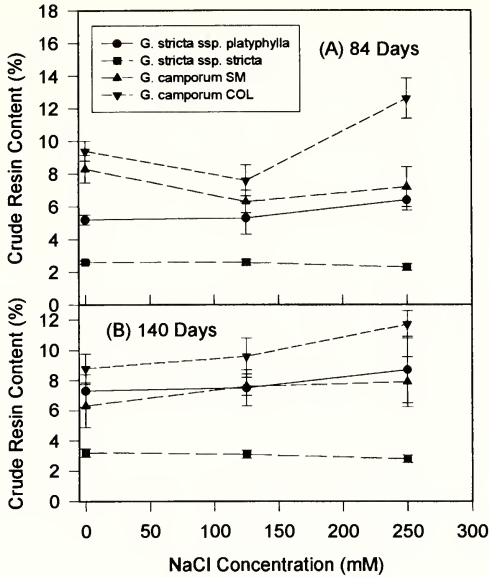


FIG. 5. Effect of NaCl on crude resin content of four *Grindelia* accessions: (A) 84 days and (B) 140 days after highest salinity was reached. Error bars represent ± 1 SE of the mean; $n=5$.

For shoots, $[Na^+]$ was higher in plants grown at 125 mM than at 5 mM NaCl but no significant differences were found between plants grown at 125 mM and 250 mM NaCl (Table 1; $P < 0.01$). $[K^+]$ and $[Ca^{2+}]$ decreased with increasing salinity ($P < 0.01$; Table 1). No significant differences were found in shoot $[Mg^{2+}]$ content or the ratio $[K^+]:[Na^+]$ between plants grown at 125 mM and 250 mM. Shoots of the four accessions differed in their $[K^+]$, $[Ca^{2+}]$ and $[Mg^{2+}]$ and in the $[K^+]:[Na^+]$ ratio. *Grindelia s. var. stricta* had higher $[K^+]$ and $[Ca^{2+}]$ than the other three accessions ($P < 0.01$), and $[Mg^{2+}]$ in *G. camporum SM* was significantly higher than in the other accessions ($P < 0.01$). Both *G. s. var. stricta* and *G. camporum SM* had higher $[K^+]:[Na^+]$ ratios than *G. s. var. platyphylla* and *G. camporum COL* ($P < 0.01$).

DISCUSSION

Accessions of *Grindelia* collected from estuary, Central Valley lowland, and foothill habitats generally responded similarly to salinity—a somewhat surprising result. All four accessions had 100% survival and positive growth rates at NaCl levels of up to 250 mM. However, survival was higher for *G. s. var. stricta* at 550 mM NaCl than for the other three accessions. Although survival rates at this NaCl concentration were very low for *G. s. var. platyphylla* and *G.*

TABLE 1. SHOOT AND ROOT CATION CONCENTRATIONS OF FOUR *GRINDELIA* ACCESSIONS GROWN UNDER THREE SALINITY LEVELS. Cation concentrations are in $\mu\text{g g}^{-1}$; salinity levels are 5, 125, and 250 mM NaCl. Means within a row (shoots and roots analyzed separately) not followed by the same letter are significantly different at $P < 0.05$.

Accession	Cation	Shoots			Roots		
		5	125	250	5	125	250
<i>G. s. var. stricta</i>	Na	101 b	695 a	781 a	490 b	805 a	759 ab
	K	1202 a	916 b	436 c	674 a	371 b	211 b
	Mg	43 a	34 b	29 b	133 a	57 b	46 b
	Ca	289 a	252 a	196 b	1446 a	880 b	77 c
	Total	1636 ab	1897 a	1441 b	2744 a	2113 b	1093 c
<i>G. s. var. platyphylla</i>	Na	106 b	772 a	886 a	318 c	752 a	548 b
	K	807 a	569 b	304 c	327 ab	495 a	206 b
	Mg	45 a	34 ab	31 b	84 a	55 b	44 b
	Ca	240 a	189 b	151 b	1753 a	1027 b	88 c
	Total	1199 b	1564 a	1373 ab	2482 a	2329 a	887 b
<i>G. camporum</i> COL	Na	105 b	671 a	744 a	273 b	582 a	724 a
	K	846 a	584 b	365 c	358 a	436 a	381 a
	Mg	47 a	38 ab	33 b	103 a	43 b	48 b
	Ca	245 a	181 b	141 b	1438 a	862 b	75 c
	Total	1252 a	1404 a	1331 a	2173 a	1923 a	1218 b
<i>G. camporum</i> SM	Na	76 b	672 a	764 a	216 b	503 a	562 a
	K	854 a	464 b	346 b	403 a	371 ab	251 b
	Mg	65 a	53 ab	47 b	79 a	48 b	48 b
	Ca	261 a	215 ab	173 b	1402 a	809 b	71 c
	Total	1252 a	1404 a	1331 a	2100 a	1731 b	931 c

camporum COL, some individuals of each accession were still able to endure sea-level salt concentration.

All accessions showed declines in dry matter production of both shoots and roots with increasing salinity. Differences were observed between coastal and inland accessions in the S:R ratios, however. We found an increase in the S:R ratio for both *G. stricta* accessions growing at 125 mM compared to those of plants at 5 mM. On the other hand, steady reductions in the S:R ratios as salinity increased were found for *G. camporum* accessions harvested at 140 days. The higher S:R ratios for the *G. stricta* accessions were an arithmetic consequence of a lower percentage reduction in their shoot biomass compared to their root biomass. We interpret these differences in S:R ratios as evidence that the estuary accessions were somewhat less stressed than the inland accessions by increasing soil salinity.

Net CO₂ uptake and transpiration were significantly reduced only at NaCl levels above 125 mM for *G. s.* var. *platyphylla* and both *G. camporum* accessions. Net CO₂ uptake and transpiration for *G. s.* var. *stricta* were not affected by NaCl concentrations up to 250 mM. Furthermore, even at 550 mM this accession maintained instantaneous values of CO₂ uptake above 10 μmol m⁻² sec⁻¹ and moderate transpiration rates. Since assimilation was not affected up to 125 mM NaCl, the decrease in biomass yield with increased salinity (from 5 mM to 125 mM) could be due to energy losses through increased respiration. Reduced biomass production accompanied by increased respiration rates at higher salinities have been found in several species (Amthor 1989).

The responses of stomatal conductance to salinity corresponded to those of CO₂ uptake and transpiration, suggesting stomatal limitations to gas exchange. Such stomatal limitations have been suggested as the main cause for reduced CO₂ uptake in other halophytes (Flanagan and Jefferies 1988). However, based on analysis of CO₂ dependence curves developed by Farquhar and Sharkey (1982), Percy and Ustin (1984) found that both stomatal and mesophyll limitations contributed to reduced CO₂ uptake in *Spartina* and *Scirpus*, two tidal-marsh plants.

Cation accumulation is a common response to increased salinity in halophytes (Flowers et al. 1977, 1986). Salt accumulation in the cell or vacuole is part of the mechanism for osmotic adjustment in these species, although high [Na⁺] in the plant can be toxic. Moderate Na⁺ accumulation is typical of miohalophytes while euhalophytes tend to accumulate large amounts of Na⁺ and maintain their [K⁺]:[Na⁺] ratios (Glenn and O'Leary 1984). In this study, we did not find an increase in cation contents in *Grindelia* grown at moderate to high NaCl levels, although significant changes in the relative proportions of cations were found. Modest accumulation of Na⁺ and a large reduction in the [K⁺]:[Na⁺] ratios in both shoots and roots

when NaCl levels increased from 5 mM to 125 mM suggest salt exclusion at the root level. Also, the extreme reduction in $[Ca^{2+}]$ content of the roots may be an indication of possible toxic effects of NaCl for *Grindelia*. Similar changes in cation composition with increased salinity within estuarine and inland *Grindelia* accessions suggest similar physiological mechanisms for coping with salt stress in these species.

Although *Grindelia* accessions were tolerant of moderate to high salinity levels, the highest biomass production for all accessions was found on fresh water. This result further serves to characterize *Grindelia* species as miohalophytes, which tolerate high salinity but show optimum growth at very low salinities, rather than euhalophytes, which require moderately high levels of salt for optimum growth (Glenn and O'Leary 1984). We expected to find differences in the responses of coastal and inland accessions to salinity. Because the estuarine species presumably are exposed to higher levels of salinity in their native habitat we expected that they would be euhalophytes, such as the *Salicornia* spp. which are found in the same community, and that the inland accessions would have a response to salinity more typical of miohalophytes. Although euhalophytes are more common in estuary environments, other estuarine species besides *G. stricta* are miohalophytes (Glenn and O'Leary 1984), including *Isocoma menziesii* (Hook. & Arn.) G. Nesom, *Hibiscus palustris* L., *Kozaletzyka virginica* (L.) Presl, and *Scirpus robustus* Pursh (Pearcy and Ustin 1984). Low salinity during the wet winter months of the growth season has been suggested to explain how *Scirpus robustus* survives in tidal marshes in California (Pearcy and Ustin 1984). In the case of *Grindelia stricta*, however, most growth occurs in the summer and fall months.

We found a variable response of crude resin production to increased salinity. At 84 days, the higher resin content in plants of both *G. camporum* accessions grown at 5 mM NaCl compared to that of plants grown at 125 mM and 250 mM could be the consequence of differences in phenological development; several of the plants grown at 5 mM had bolted producing stems and capitula-buds, while only one *G. camporum* (both accessions) plant had bolted at 125 mM. The difference in phenological stages may have resulted in the high resin content found in low salinity plants, since the capitula of *G. camporum* have resin contents up to 20–30% while leaves and stems are lower in resin (less than 10%) (Timmermann and Hoffmann 1985). On the other hand, the higher resin content of *G. camporum* (both accessions) grown at 250 mM compared to those at 125 mM was found in plants at similar phenological stages and thus could be a true response to salinity.

By the time of the second harvest, both accessions of *G. camporum* had bolted at all salinity levels, although the number of plants with inflorescences and the number of inflorescences per plant de-

creased with increased salinity. Any direct effect that NaCl could have on resin production (i.e., the trend of increased resin at higher salinity for *G. camporum* COL in Fig. 5b) would be masked by differences in the number of capitula produced. In this experiment our primary objective was to compare salt tolerance and biomass production, and to accomplish this objective plants were harvested at the same time. To further study the effects of NaCl on resin production, harvests should be done according to phenological stages (i.e., at peak flowering).

Grindelia s. var. stricta did not show any significant change in resin content with salinity. Although the dichloromethane extract has been termed "crude resin", this accession has a very low proportion of resin acids in the DCM extract (Timmermann et al. 1987). The ecological significance of the low crude resin yield and the small proportion of diterpene acids in the extract for this species is not clear to us.

There are several implications from this study for the development of *Grindelia* as a potential crop for saline soils. First, *Grindelia camporum* is able to tolerate moderate to high levels of NaCl, but biomass production is reduced at salt levels around one fourth that of sea water. Such reduced biomass production would sharply decrease the economic attractiveness of this plant as a crop for saline soils. Second, there would seem to be no advantage in hybridizing inland or foothill *G. camporum* with coastal *G. stricta* and selecting among the progeny as a means for improving the salt tolerance of *G. camporum*, since the two species appeared to be fairly similar in their responses to increased salinity. Any slight gain in salt tolerance probably would be achieved at the cost of greatly reduced resin yield. Finally, we observed a slight increase in resin production at higher salinity levels. Information on the effect of NaCl on the secretion of secondary metabolites is very scarce. Hajibagheri et al. (1983) found thicker, larger wax plates in the surface of *Suaeda maritima* leaves grown with sodium chloride. Increased production of secondary metabolites in response to stress has been reported for other plants as well (Allen et al. 1987; Benzioni et al. 1989; Vaadia et al. 1961). In this experiment we found evidence that supports this proposition, although further experiments should be conducted in order to thoroughly evaluate the response of surface resin production to NaCl.

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